DIFFERENTIAL RESPONSES TO NITROGEN FORM AND CONCENTRATION FOR *ORYZOPSIS HYMENOIDES* AND *ELYMUS LANCEOLATUS*

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Abstract.—In a greenhouse experiment, effects of nitrogen form and concentration on productivity and dry matter allocation differed between two species native to semiarid ecosystems of the Great Basin. Aboveground production of green surface area and of dry matter were consistently enhanced by increased nitrogen for the rhizomatous grass *Elymus lanceolatus*, but not for the bunchgrass *Oryzopsis hymenoides*. These differences were likely due to inherently low growth rates of *O. hymenoides*. Aboveground dry matter allocation also differed between the two species. *O. hymenoides* had more leaves per tiller with increased nitrogen, whereas leaf size but not number increased for *E. lanceolatus*. Furthermore, increases in tiller density with increased nitrogen for *E. lanceolatus* were almost three times greater than those for *O. hymenoides*. *E. lanceolatus*, but not *O. hymenoides*, was sensitive to the form of nitrogen supplied to the plants. When NH_4–N was the only form of nitrogen supplied, high concentrations of NH_4–N inhibited aboveground production of *E. lanceolatus*.

Key words: dry matter production, dry matter allocation, ammonium-N, nitrate-N, nitrogen use efficiency, relative growth rate, Oryzopsis hymenoides, Elymus lanceolatus.

Water availability is generally acknowledged to be the abiotic factor that most limits productivity of semiarid vegetation (MacMahon and Schimpf 1981, Skujins 1981), and nitrogen is thought to be the second-most limiting factor (James and Jurinak 1978, Skujins 1981). However, evidence from field fertilization experiments that nitrogen limits productivity is not conclusive (Smith and Nowak 1990). Procedural problems may be partially responsible for the lack of a response to nitrogen fertilization in field trials. For example, low rates of application (James and Jurinak 1978, Fairbourn and Ranzi 1982) may not be sufficient to stimulate a statistically significant effect. Because the form of nitrogen affects plant growth (Bollard 1966, Smith et al. 1983), the form of nitrogen applied can also affect the vegetation responses. Of greater interest are biological and ecological processes that may influence the response of vegetation to fertilization. These processes include (1) loss of fertilizer nitrogen by volatilization or other processes (Klubek et al. 1978, Westerman and Tucker 1978), (2) inherently low growth rates of plants that inhabit low nutrient environment (Chapin 1980), and (3) inherent differences among species in their responses to fertilization (Fisher and Hay 1987).

Differentiating between procedural problems and ecological processes has made it difficult to clearly elucidate the relationships between plant productivity and the form or supply of nitrogen for plants in a natural, semiarid environment. However, experimentation in controlled environments minimizes problems associated with field experiments such as the following: (1) other growth conditions are optimized, (2) a range of application rates can be readily used, (3) different forms of nitrogen can be easily applied, and (4) individual responses of different species can be determined. Thus, we conducted a glasshouse experiment to determine the effects of nitrogen form and application rate on dry matter (DM) production and allocation for some representative Great Basin species.

Two forage grasses that are widely distributed throughout semiarid rangelands in the Great Basin and that represent two of the major growth forms of grasses were selected for this study: *Oryzopsis hymenoides* (R. & S.) Ricker and *Elymus lanceolatus* (Scribn. & J. G. Smith) Gould. Although the geographic distributions of these two species differ, they can occur together in native stands where their distributions overlap. *O. hymenoides* is a perennial bunchgrass that grows in cold-

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desert environments that receive less than 100 mm annual precipitation to over 200 mm (Robertson 1976, Jones 1990). Like *O. hymenoides*, *E. lanceolatus* is a native, perennial, drought-tolerant grass, but *E. lanceolatus* has a rhizomatous growth form. *E. lanceolatus* previously was known as *Agropyron dasystachyum* (Barkworth and Dewey 1985), and many authors also treat *E. lanceolatus* and *A. riparium* as synonyms (Hitchcock and Cronquist 1973, Cronquist et al. 1977, Barkworth and Dewey 1985). Because it was impractical to transplant *E. lanceolatus* plants into pots for our greenhouse experiment, a cultivar of *E. lanceolatus* called Sodar was used. Sodar is a naturally occurring variety that was released in 1954 as a special-purpose grass to provide groundcover rather than forage (Douglas and Ensign 1954). Sodar has been widely used for revegetation in the area from which we collected the *O. hymenoides* plants used for transplanting.

The primary objective of our study was to determine the effects of nitrogen form and application rate on DM production and allocation for these two semiarid species. Because DM production may also increase the surface area available for photosynthesis, we also measured green surface area. DM allocation was analyzed as changes in tiller production, number of leaves per tiller, leaf DM, sheath/stem DM, and root DM.

METHODS

Plant Establishment

Plants of *O. hymenoides* and *E. lanceolatus* were established in 12-L pots at plant densities that were representative of natural field conditions. Initial plant densities were 1 plant per pot for *O. hymenoides* and 15 per pot for *E. lanceolatus*. Pots were filled with clean sand, and 40 pots of each species were used. Plants of *O. hymenoides* were originally collected from the U.S. Department of Energy, Idaho National Engineering Laboratory, in late fall. The previous summer's growth had senesced by this time, and plants were dormant. One *O. hymenoides* plant was transplanted into each pot. Seeds of *E. lanceolatus* cv Sodar were germinated in petri dishes, and 15 seedlings were planted into each pot. All pots were placed in a greenhouse, where the experiments were conducted. Greenhouse air temperature varied from 20°C at night to 30°C during the day. Plants received only solar irradiance, which typically peaked at a photosynthetic photon flux density (PPFD) of 1.1 mmol m^{-2} s^{-1}.

After two months of growth, each species was sorted into four size classes based upon the number of tillers in the pot. Two replicates from each size class were randomly selected for a pretreatment destructive harvest (total sample size of eight pots per species). The remaining 32 replicates of each species were assigned to the eight nitrogen treatments with a stratified-random technique to insure adequate interspersion (Hurlbert 1984). At the initiation of the experiment, the pots with *O. hymenoides* had 62.1 ± 3.8 tillers per pot (average ± standard error) with 2.6 ± 0.1 green leaf blades (leaves) per tiller, whereas *E. lanceolatus* had 13.3 ± 0.3 tillers per pot with 5.2 ± 0.1 leaves per tiller.

Nutrient Solution Treatments

Ruakura nutrient solution (Smith et al. 1983) was selected for these experiments because pasture plants grown in Ruakura solution consistently yielded more DM than those grown in seven other nutrient culture solutions. The Ruakura solution has a 1:3 ratio of NH_4–N to NO_3–N, and concentrations of other nutrients do not appear to limit plant growth or to accumulate in toxic proportions. Eight experimental treatments were used that varied both the concentration and form of nitrogen (Table 1). Four concentrations of nitrogen with both forms of nitrogen in the nutrient solution were used: 25% (0.25), 50% (0.5), 100% (1.0), and 200% (2.0) of the full-strength concentration of nitrogen. In addition, two concentrations (0.25 and 2.0 of the full-strength nitrogen concentration) were used for solutions either with NH_4–N as the only nitrogen form or with NO_3–N as the only nitrogen form.

For our experiments, only the concentration of nitrogen in the nutrient solution was changed. The concentration of most other ions was held constant, as opposed to varying the concentration of all other ions in concert with nitrogen. To maintain the proper concentrations of the other nutrients, calcium, carbonate, and chloride salts were used as needed to prepare the nutrient solutions. Pots received 750-ml applications of the nitrogen solution

ions that were constant in all nutrient solutions.

Macronutrients			Micronutrients		
K	=	238	Fe	=	3.0
S	=	60	B	=	0.5
P	=	10	Mn	=	0.5
Mg	=	21	Zn	=	0.25
Na	=	15	Cu	=	0.04
			Mo	=	0.01

Macronutrients whose concentration varied with different nutrient solutions:

Nutrient solution					
N[a]	Form of nitrogen	NO_3–N	NH_4–N	Ca	Cl
2.0	NH_4–N + NO_3–N	396	132	308	9
1.0	NH_4–N + NO_3–N	198	66	127	9
0.5	NH_4–N + NO_3–N	99	33	127	9
0.25	NH_4–N + NO_3–N	49.5	16.5	127	102
2.0	NO_3–N only	528	0	685	9
0.25	NO_3–N only	66	0	127	89
2.0	NH_4–N only	0	528	127	224
0.25	NH_4–N only	0	66	127	224

[a] Amount of total nitrogen in nutrient solution relative to full-strength Ruakura.

twice weekly, and applications of nutrient solutions were alternated with tap watering.

Pretreatment Productivity Measurements

Dimensional measurements were used to estimate initial DM compartments of the treatment pots. Three tillers from each *E. lanceolatus* pot and five from each *O. hymenoides* pot were randomly selected for destructive harvest; more tillers were sampled from *O. hymenoides* because those pots had more tillers. The number of green leaves per tiller was counted, and the total length of all green leaves on a tiller and of all green sheaths and stems on a tiller was measured. For the eight pots of each species that were selected for the pretreatment harvest, projected areas and dry weights of leaves and of sheaths/stems on these same tillers were also measured.

Relationships between length and both area and weight were computed. Power regressions of length versus either area or weight had higher R^2 values than simple linear or log-linear regressions for *O. hymenoides*. A simple linear regression with an intercept of zero had the highest R^2 values for *E. lanceolatus*. The *F* tests for all regression equations were significant; *P* was less than .001 for each regression. R^2 values averaged .88 for the eight regressions, with a range of .70–.98. These equations were then used to estimate the initial, pretreatment leaf area, leaf DM, sheath/stem area, and sheath/stem DM per tiller for the treatment pots. Total green area per tiller and total DM per tiller were calculated by summing the leaf and sheath/stem fractions. The initial leaf area index (LAI) of each treatment pot was estimated by multiplying the mean total area per tiller for that pot by the total number of tillers in that pot. Initial standing crop was the product of the mean total DM per tiller and the total number of tillers in that pot. Both LAI and standing crop were expressed on a pot area basis.

None of the pretreatment measurements of area or DM were significantly different among the experimental groups for both species (data not shown). Thus, replicate pots were adequately stratified among the experimental groups before the initiation of the treatments, and posttreatment differences among treatments can be attributed to effects of the nutrient solution rather than to initial differences in the experimental groups.

Posttreatment Productivity Measurements

Aboveground standing crop at the end of the experiment for each pot was determined

with both destructive harvest and estimation techniques. We measured the number of green leaves per tiller as well as green leaf and green sheath/stem areas for three *E. lanceolatus* and five *O. hymenoides* randomly selected tillers. We also measured dry weights of both green and dead fractions for leaves and sheath/stems for these same tillers. Total green area per tiller and total (green plus dead) DM per tiller were calculated by summing the leaf and sheath/stem compartments. Posttreatment LAI and standing crop for each pot were estimated in the same manner as pretreatment values. Relative growth rates (RGR) of DM and of tillers were calculated from the pretreatment and posttreatment measurements of DM per tiller, standing crop, and number of tillers per pot. RGR was computed using the classical interval equation (Chiariello et al. 1989).

Three soil samples were taken from the center of each pot to determine belowground standing crop. Each sample was 237 ml (8 oz), and samples were taken from near the top of the soil surface, the middle of the soil profile, and near the bottom of the pot. The three samples were composited, and organic matter and soil particles were separated with a "root washer" (Smucker et al. 1982). Live roots were then separated from dead organic matter by a staining technique (Ward et al. 1978), dried, and weighed.

Plant and Soil Chemical Analyses

Total nitrogen concentrations for the green leaf, green sheath/stem, and senesced tissue compartments were determined with a CHN analyzer (Perkin-Elmer Model 2400). All green leaves on the three *E. lanceolatus* tillers that were harvested in each pot were pooled together, then ground to 40-mesh size. Similarly, all green sheath/stem and senesced tissue fractions from *E. lanceolatus* tillers as well as green leaf, green sheath/stem, and senesced fractions for the five *O. hymenoides* tillers were pooled and ground. The nitrogen concentration of each fraction was multiplied by the respective dry weight, and those products were then summed to calculate a total weight of nitrogen, or nitrogen pool size, per tiller. Tiller nitrogen pool size was multiplied by the total number of tillers in that pot to determine nitrogen standing crop for each pot. Finally, the amount of aboveground DM produced per unit of aboveground nitrogen uptake, which we term nitrogen use efficiency (NUE), was calculated from the ratio of posttreatment standing crop minus initial standing crop to posttreatment nitrogen standing crop minus initial nitrogen standing crop.

To determine soil properties, we took a second set of soil samples adjacent to the root samples. Soil analyses were conducted by the Soil Analysis Laboratory of the Nevada Agricultural Experiment Station using standard techniques. Electrical conductivity (EC) and pH of the soil water were determined following the methods of Richards (1954). Ca, Mg, and Na were determined on saturation extracts with an atomic absorption spectrometer (Perkin-Elmer Model 5000). Total nitrogen in the soil was determined with Kjeldahl analysis modified to include NO_3–N. These same soil chemical properties were also determined for soil samples taken from the pretreatment, destructive harvest pots.

Statistical Analyses

Analysis of variance (AOV) techniques were used for data analyses. One-way AOVs were used to determine if pretreatment DM measurements differed among the eight experimental groups. Posttreatment soil chemical properties and plant productivity were analyzed with a two-step procedure because our experimental design had missing cells; i.e., the two intermediate nitrogen concentrations were not used for the solutions with NH_4–N only or with NO_3–N only. The first statistical analysis was to determine the interactive effects of nitrogen form and concentration on DM production and allocation. Each species was analyzed with separate two-way AOVs. Each AOV had two main effects: nitrogen form in the nutrient solutions (three levels: NO_3–N only, NH_4–N only, and both forms) and nitrogen concentration in the nutrient solutions (two levels: 0.25 and 2.0). For significant terms in the AOVs, means were compared with LSD techniques, taking into account the appropriate precautions (Snedecor and Cochran 1967). The second statistical analysis had two objectives: first, to determine if DM production and allocation changed linearly with the concentration of nitrogen in the nutrient solution; and second, to determine if this relationship differed between the two species. Split-plot AOVs

with covariance analysis and linear contrasts were used in this second step. Nitrogen concentration in the nutrient solutions (four levels: 0.25, 0.5, 1.0, and 2.0) was the main plot treatment factor, with species (two levels) as a split-plot factor. Because of the initial differences between species, pretreatment area and DM measurements were used as covariates for each respective posttreatment variable. Coefficients for the linear contrasts were calculated according to procedures described in Gomez and Gomez (1984). For all statistical analyses, $P < .05$ was considered significant.

RESULTS

Effects of Solution Nitrogen Form on Productivity

DM PRODUCTION AND ALLOCATION.—The form of nitrogen influenced aboveground productivity and allocation of *E. lanceolatus* but did not significantly affect root DM nor root:shoot ratios (Table 2). The effects of nitrogen form on DM production and allocation occurred primarily at the high concentration of nitrogen. Although the nitrogen form main effect was significant for only the four measurements of green surface area, all but four of the dependent variables had a significant interaction term. For each of the dependent variables that had a significant interaction term in the 2-way AOV, DM production for pots supplied either with both forms of nitrogen or with NO_3–N only increased with increased nitrogen concentration. However, the corresponding measurement of DM production for pots supplied with the 0.25 NH_4–N only nitrogen solution was not significantly greater than that for pots supplied with the 2.0 NH_4–N only nitrogen solution. Thus, close inspection of the interaction terms showed that inhibitory effects of nitrogen form occurred only if a high concentration of NH_4–N was the sole source of nitrogen.

The form of nitrogen did not affect DM production or allocation of *O. hymenoides* (data not shown). Neither the interaction term nor the nitrogen form main effect was significant in the 2-way AOVs for the same 15 variables listed for *E. lanceolatus* in Table 2.

TISSUE NITROGEN CONTENT AND NITROGEN USE EFFICIENCY.—For *O. hymenoides*, the effects of the form of nitrogen varied among the different nitrogen compartments (Table 3). The main effect of nitrogen form was not significant for the concentration of nitrogen in green sheath/stem tissue, the total pool size of nitrogen in a tiller, and the total aboveground pool size of nitrogen in a pot. For senesced tissue, mean nitrogen concentration of tissue from pots that received both forms of nitrogen was significantly lower than that for plants that received only one form of nitrogen. For green leaf tissue, tissue nitrogen concentration for plants that received either both forms of nitrogen or NO_3–N only was significantly lower than that for plants that received NH_4–N only. However, NUE of plants that received NH_4–N only was significantly lower than NUE of those that received either both forms of nitrogen or NO_3–N only.

For *E. lanceolatus*, the form × concentration interaction terms were significant for four of the six nitrogen compartments: leaf nitrogen concentration, tiller nitrogen content, nitrogen standing crop, and NUE (Table 3). For these four compartments, means for different forms of nitrogen in the 0.25 nutrient solutions were not significantly different. For the 2.0 nutrient solutions, means for leaf nitrogen concentration, tiller nitrogen content, and nitrogen standing crop with both forms of nitrogen were significantly greater than means for those compartments either with NH_4–N only or with NO_3–N only. Mean NUE with both forms of nitrogen was, however, significantly less than that with NH_4–N only or NO_3–N only. The main effect of nitrogen form was significant for nitrogen concentration of senesced tissue: mean concentration for pots that received NH_4–N only was significantly greater than for pots that received NO_3–N only, but the mean for pots that received both forms of nitrogen solution was not significantly different from the other two means.

Effects of Solution Nitrogen Concentration on Productivity

DM PRODUCTIVITY AND ALLOCATION.—The effects of increased nitrogen concentration on green surface area and DM production were significantly greater for *E. lanceolatus* than for *O. hymenoides* (Fig. 1). Over the range of nitrogen concentrations used, both green area and DM of *E. lanceolatus* increased linearly with nitrogen concentration for measurements on a leaf, tiller, and ground area basis (Figs.

TABLE 2. AOV, means, and mean comparisons for effects of nitrogen form at two levels of nitrogen concentration on DM compartments of *E. lanceolatus*.

	AOV table[a]			Means[b]					
	Main effects			0.25 N solution			2.0 N solution		
DM compartment	N form	N conc	Interaction	A+N	A only	N only	A+N	A only	N only
Green sheath/stem area (cm^2 $tiller^{-1}$)	0.042	0.001	0.008	0.44*a*	0.54*a*	0.54*a*	1.11*b*	0.49*a*	0.90*b*
Green leaf area (cm^2 $tiller^{-1}$)	0.001	0.012	0.001	10*a*	11*ab*	15*bc*	20*d*	8*a*	17*cd*
Total green surface area (cm^2 $tiller^{-1}$)	0.001	0.010	0.001	10*a*	12*ab*	15*bc*	21*d*	9*a*	18*cd*
Leaf area index	0.002	<0.001	<0.001	7*a*	11*ab*	13*b*	26*d*	9*ab*	20*c*
Green sheath/stem DM (mg $tiller^{-1}$)	NS	NS	NS	10	60	16	30	13	20
Green leaf DM (mg $tiller^{-1}$)	NS	0.040	0.004	55*a*	73.3*ab*	80*ab*	114*c*	57*a*	90*bc*
Total (green + dead) DM (mg $tiller^{-1}$)	NS	NS	0.006	90*a*	162*b*	131*ab*	179*b*	88*a*	151*ab*
Standing crop (kg m^{-2})	NS	0.005	<0.001	0.6*a*	1.4*bc*	1.1*abc*	2.3*d*	0.9*ab*	1.6*cd*
Root DM (g l^{-1})	NS	NS	NS	1.8	4.2	4.2	3.1	1.1	5.0
Root:shoot ratio	NS	0.003	NS	1.83	0.82	0.93	0.30	0.31	0.71
Number of green leaves per tiller	NS	NS	NS	1.4	4.6	4.6	4.4	4.6	4.5
Tiller density (number cm^{-2}	NS	<0.001	0.035	0.66*a*	0.89*ab*	0.84*ab*	1.30*c*	1.02*b*	1.11*bc*
Tiller DM RGR (mg g^{-1} day^{-1})	NS	NS	0.001	20*ab*	26*bc*	24*abc*	30*c*	19*a*	25*bc*
Crop DM RGR (mg g^{-1} day^{-1})	NS	0.001	<0.001	61*a*	71*c*	69*bc*	80*d*	66*ab*	72*c*
Tiller number RGR (% day^{-1})	NS	<0.001	0.001	4.1*a*	4.5*b*	4.5*b*	5.0*d*	4.7*bc*	4.8*cd*

[a] *P* values for the two main effects and the interaction term from 2-way AOVs. NS indicates the term was not significant ($P > .05$).

[b] Means for pots that received both forms of nitrogen (A+N), that received NH_4 N only (A only), and that received NO_3 N only (N only). Means within a row with the same letter were not significantly different.

Table 3. AOV results and mean comparisons for effects of nitrogen form at two levels of nitrogen concentration on nitrogen content of DM compartments and nitrogen use efficiency for *O. hymenoides* and *E. lanceolatus*.

	AOV table[a]			Means[b]					
	Main effects			0.25 N solution			2.0 N solution		
Nitrogen compartment	N form	N conc	Interaction	A+N	A only	N only	A+N	A only	N only
O. hymenoides									
Senesced tissue N concentration (%)	0.017	0.035	NS	1.1	1.5	1.5	1.4	1.9	1.7
Sheath/stem N concentration (%)	NS	NS	NS	2.1	2.2	2.6	2.6	2.6	2.1
Leaf N concentration (%)	0.001	<0.001	NS	3.8	4.5	3.8	4.7	5.5	4.5
Tiller N content (mg tiller^{-1})	NS	0.027	NS	2.4	2.5	1.9	2.6	3.1	2.9
N standing crop (g m^{-2})	NS	0.001	NS	9	12	11	15	20	18
Nitrogen use efficiency (g DM g^{-1} N)	0.001	<0.001	NS	46	32	42	31	25	30
E. lanceolatus									
Senesced tissue N concentration (%)	0.029	<0.001	NS	1.0	1.1	1.0	2.1	2.3	1.7
Sheath/stem N concentration (%)	NS	<0.001	NS	1.7	1.7	1.7	2.4	2.1	2.5
Leaf N concentration (%)	<0.001	<0.001	<0.001	3.1*ab*	2.8*a*	3.1*ab*	4.7*c*	3.1*ab*	3.2*b*
Tiller N content (mg tiller^{-1})	0.020	0.002	<0.001	2.1*a*	3.5*ab*	3.1*ab*	6.8*c*	2.4*a*	4.0*ab*
N standing crop (g m^{-2})	0.002	<0.001	<0.001	14*a*	30*ab*	26*a*	86*c*	24*a*	44*b*
Nitrogen use efficiency (g DM g^{-1} N)	0.001	<0.001	0.010	43*c*	47*c*	43*c*	26*a*	37*b*	37*b*

[a]*P* values for the two main effects and the interaction term from 2-way AOVs. NS indicates that the term was not significant ($P > .05$).
[b]Means for pots that received both forms of nitrogen (A+N), that received NH_4–N only (A only), and that received NO_3–N only (N only). Means within a row with the same letter were not significantly different

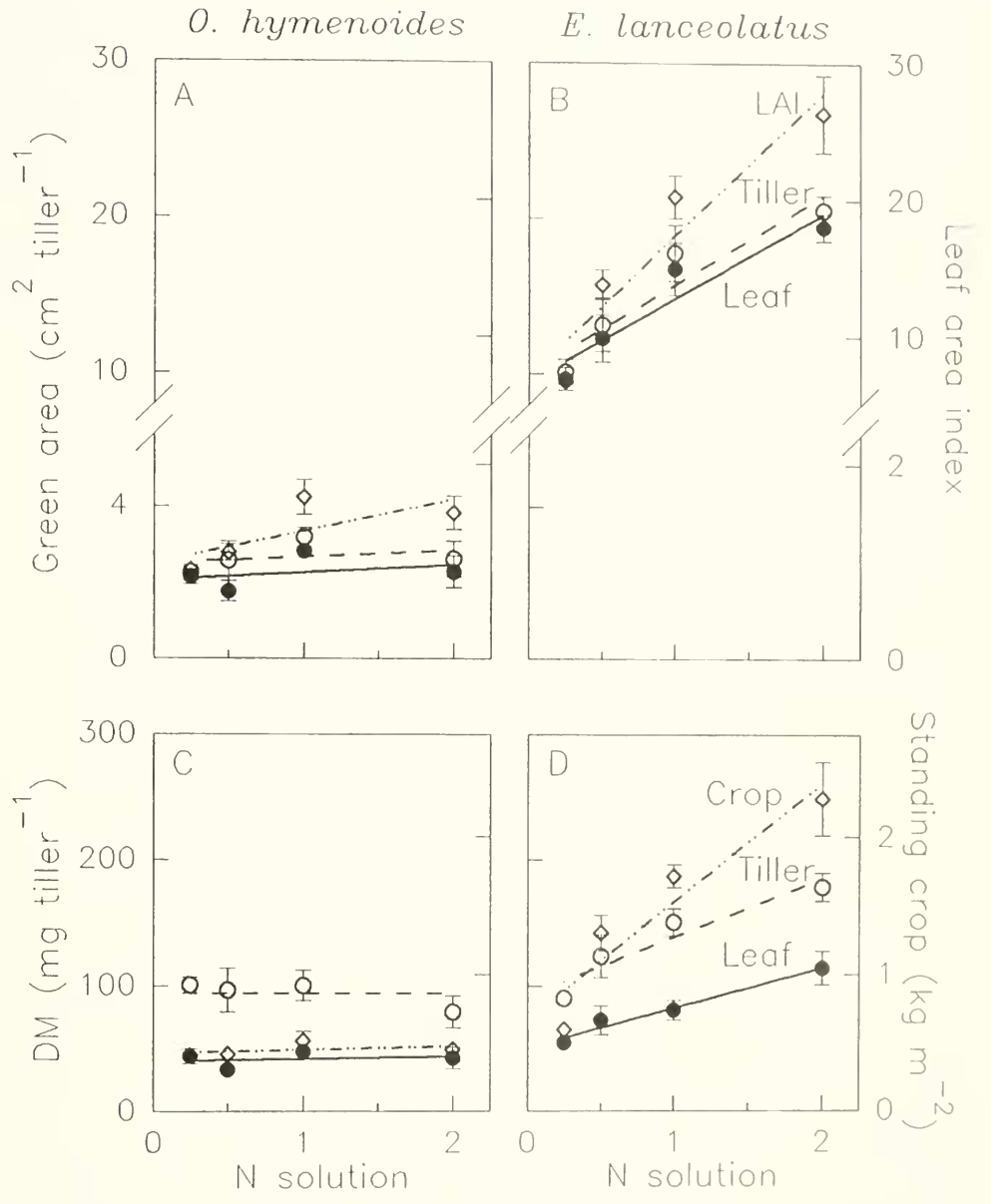

Fig. 1. Aboveground green surface area and DM for *O. hymenoides* (A, C) and *E. lanceolatus* (B, D) at the end of the greenhouse experiment. Means and standard error bars at each concentration of nitrogen in the nutrient solution are given. A, B: Green leaf area per tiller (solid circles, solid lines), total green area per tiller (open circles, dashed lines) and green leaf area index (diamonds, dash-dot-dot lines). C, D: Leaf DM per tiller (solid circles, solid lines), total DM per tiller (open circles, dashed lines), and aboveground standing crop (diamonds, dash-dot-dot lines). Lines are linear regressions of the data if linear contrasts were significant or horizontal lines if the linear contrasts were not significant

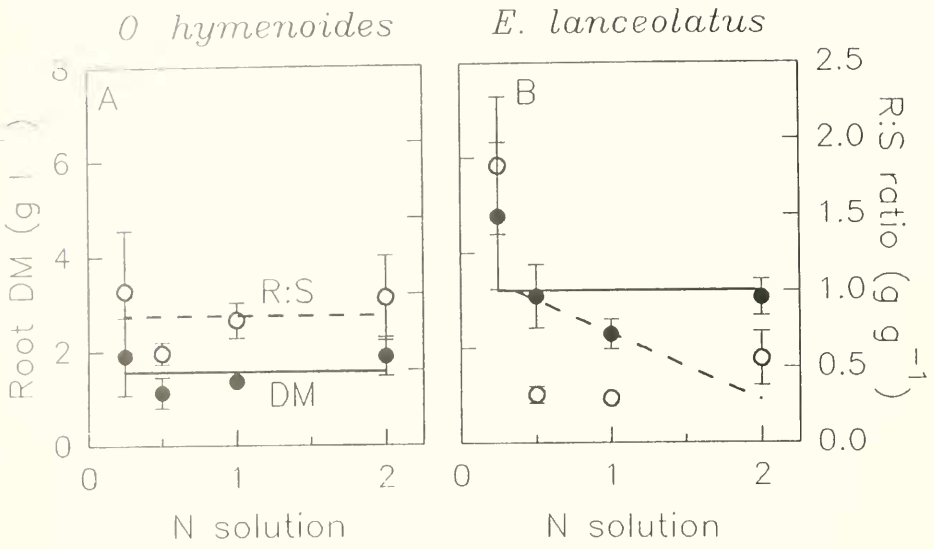

Fig. 2. Belowground DM for *O. hymenoides* (A) and *E. lanceolatus* (B) at the end of the experiment. A, B: Root DM (solid circles, solid lines) and root:shoot ratio (open circles, dashed lines). Other graph characteristics are as given in Figure 1.

1B, 1D). Although the linear contrasts of the three area measurements with nitrogen concentration were significant for *O. hymenoides* (Fig. 1A), these increases in surface area with nitrogen concentration were much less than those for *E. lanceolatus* (Fig. 1B). For the DM compartments of *O. hymenoides* (Fig. 1C), linear contrasts were significant for leaf and standing crop DM, but not for tiller DM.

Root DM was not affected by nitrogen concentration in either species (Figs. 2A, 2B). Root DM for *E. lanceolatus*, however, was significantly greater than that for *O. hymenoides* at all nitrogen concentrations. Root:shoot (R:S) ratios of *E. lanceolatus* significantly decreased with increased nitrogen concentration, whereas those of *O. hymenoides* were unaffected by nitrogen concentration. Although R:S ratios were not significantly different between species at low nitrogen concentrations, they were significantly greater for *O. hymenoides* at high nitrogen concentrations.

Tiller density increased with increased nitrogen concentration for both species (Fig. 3). Tillers of *O. hymenoides* grown at high nitrogen concentrations also had more green leaves per tiller than those grown at low nitrogen concentrations (Fig. 3A). However, the number of leaves per tiller for *E. lanceolatus* was unaffected by nitrogen concentration (Fig. 3B). Finally, both tiller density and number of green leaves per tiller for *E. lanceolatus* were significantly greater than those for *O. hymenoides*.

Except for DM per tiller for *O. hymenoides* (Fig. 4A), increased nitrogen concentration increased RGR (Fig. 4). In addition, RGR of DM on a tiller basis, of DM on a crop basis, and of tiller number for *E. lanceolatus* (Fig. 4B) were significantly greater than those for *O. hymenoides* (Fig. 4A).

TISSUE NITROGEN CONTENT AND NITROGEN USE EFFICIENCY.—The concentration of nitrogen had a significant effect on tissue nitrogen concentration of both species (Figs. 5A, 5B). Tissue nitrogen concentrations increased with increased concentration of nitrogen. Nitrogen concentrations of green tissues were significantly greater for *O. hymenoides* than for *E. lanceolatus* except at the highest solution nitrogen concentration. For senesced tissue, tissue nitrogen concentrations were similar for both species at low solution nitrogen concentrations, but *E. lanceolatus* had significantly higher tissue nitrogen concentrations than *O. hymenoides* at the high solution nitrogen concentration.

Aboveground pool sizes of tissue nitrogen significantly increased with solution nitrogen

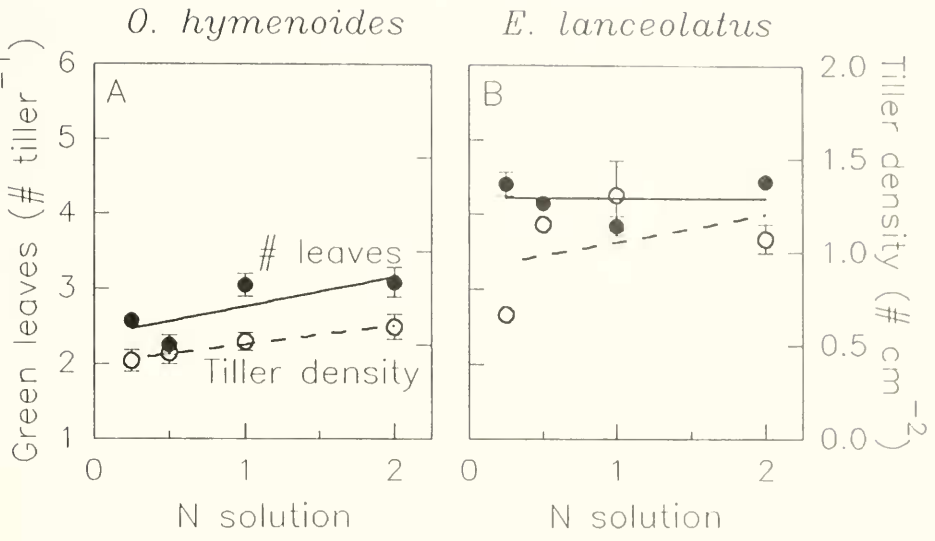

Fig. 3. Number of green leaves per tiller (solid circles, solid lines) and tiller density (open circles, dashed lines) for *O. hymenoides* (A) and *E. lanceolatus* (B) at the end of the experiment. Other graph characteristics are as given in Figure 1.

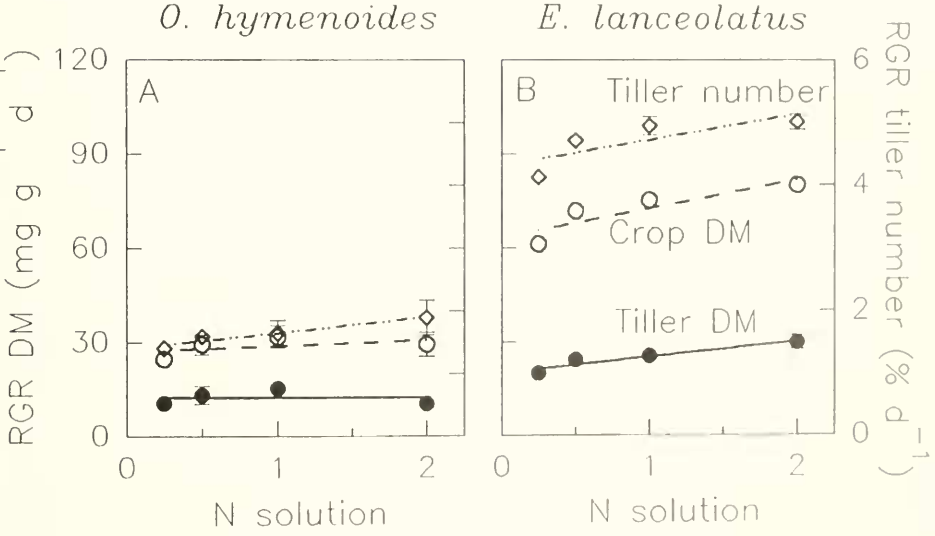

Fig. 4. Relative growth rates for *O. hymenoides* (A) and *E. lanceolatus* (B) over the duration of the experiment. Mean RGRs at each level of nitrogen concentration in the nutrient solution are given for DM production per tiller (solid circles, solid lines), total aboveground DM production (open circles, dashed lines), and number of tillers (diamonds, dash-dot-dot lines). Other characteristics of the graph are as given in Figure 1.

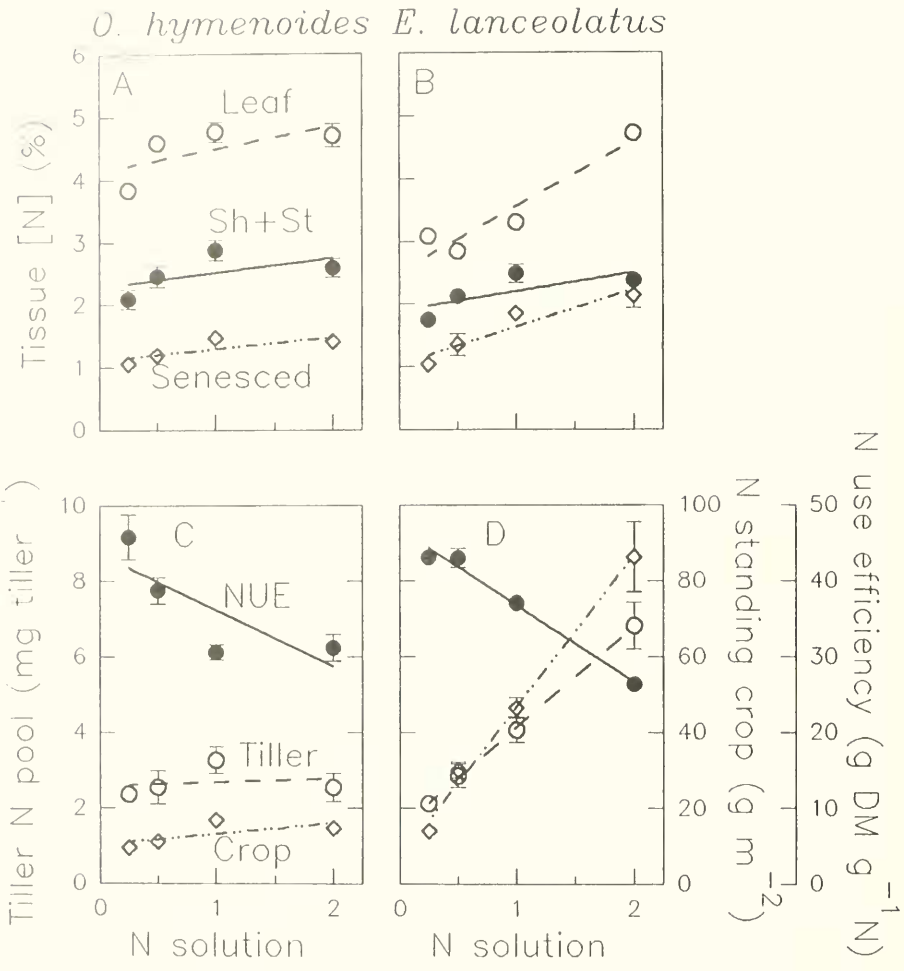

Fig. 5. Nitrogen concentrations, pool sizes, and use efficiencies for aboveground DM for *O. hymenoides* (A, C) and *E. lanceolatus* (B, D). A, B: Nitrogen concentrations of leaves (open circles, dashed lines), sheaths/stems (solid circles, solid lines), and senesced tissues (diamonds, dash-dot-dot lines). C, D: Total pool size of nitrogen in tillers (open circles, dashed lines), total pool size of nitrogen in the aboveground standing crop (diamonds, dash-dot-dot lines), and nitrogen use efficiency (solid circles, solid lines). Other graph characteristics are as given in Figure 1.

concentration for both species, but NUE decreased with increased solution nitrogen concentration (Figs. 5C, 5D). Nitrogen pool sizes, expressed either as the total amount of nitrogen per tiller or as the total amount of nitrogen in the crop, were not significantly different between species at low solution nitrogen concentrations, but nitrogen pool sizes at high solution nitrogen concentrations for *E. lanceolatus* were significantly greater than those for *O. hymenoides*. NUE, i.e., the amount of aboveground DM produced per amount of nitrogen uptake, was not significantly different between species.

Soil Chemical Properties

The form and concentration of nitrogen in the nutrient solution had only minor effects on soil chemical properties. Of particular interest was soil pH. Nitrogen form significantly affected the pH of soils from *O. hymenoides* pots: pH of soils that received both forms of nitrogen (7.6) was slightly but significantly lower than pH of soils that received either NH_4–N only (7.8) or NO_3–N only (7.9). Small but significant differences in pH among nitrogen-concentration groups also occurred, but only for soils from *E. lanceola-*

TABLE 4. Pretreatment (Pretrt) and posttreatment chemical properties of soil samples composited from each pot and analyzed by standard soil techniques.

		Nitrogen solution[a]			
Edaphic property	Pretrt	0.25	0.5	1.0	2.0
O. hymenoides					
pH	7.6	7.8	7.7	7.8	7.7
Cations					
Ca (meq l^{-1})	4.0	9.5*a*	6.2*a*	20.4*a*	39.9*b*
Mg (meq l^{-1})	0.8	2.4*a*	1.6*a*	4.5*b*	1.9*b*
Na (meq l^{-1})	1.6	2.8	2.3	3.6	2.6
EC (dS m^{-1})	0.4	1.2*a*	0.9*a*	2.2*a*	5.1*b*
Nitrogen					
Total N (μg g^{-1})	71	138*a*	273*a*	689*a*	1535*b*
E. lanceolatus					
pH	8.2	8.0*b*	8.3*c*	8.5*c*	7.8*a*
Cations					
Ca (meq l^{-1})	3.4	7.3*a*	5.3*a*	11.7*a*	21.3*b*
Mg (meq l^{-1})	0.7	1.7	1.4	2.4	2.9
Na (meq l^{-1})	1.5	2.9*a*	4.2*b*	3.0*ab*	2.3*a*
EC (dS m^{-1})	0.5	1.0*a*	1.2*a*	1.4*ab*	2.2*b*
Nitrogen					
Total N (μg g^{-1})	82	69*a*	78*a*	408*b*	773*c*

[a]Statistical differences among posttreatment means are indicated by different letters in a row; rows without letters indicate that the AOV terms were not significant

tus pots (Table 4). For both species, Ca concentration was significantly greater only at the highest nitrogen concentration (Table 4), but nitrogen form did not affect Ca concentration (data not shown). Except for total soil nitrogen, the effects of form (data not shown) and concentration (Table 4) of solution nitrogen were either not significant or significant but of small magnitude. Total soil nitrogen significantly increased with increased concentration of nitrogen in the nutrient solution for both species (Table 4).

DISCUSSION

Effect of Solution Nitrogen Form on Productivity

Aboveground DM production and allocation for *E. lanceolatus* were sensitive to the form of nitrogen in the nutrient solution, whereas those for *O. hymenoides* were not. This sensitivity of *E. lanceolatus* to nitrogen form does not appear to be induced by soil pH. Productivity can be inhibited by acidification of the substrate in the presence of NH_4–N (Thomas et al. 1987) accompanied by a low pH-induced inhibition of NH_4–N uptake (Vessey et al. 1990), but pH of soils from *E. lanceolatus* pots was slightly alkaline and not significantly affected by the form of nitrogen in the solution. More likely, this sensitivity to nitrogen form in *E. lanceolatus* is due to some species-specific characteristics of nutrient uptake or assimilation. For example, *E. lanceolatus* may have a low level of glutamine synthetase activity, which detoxifies NH_4–N in plants (Magalhaes and Huber 1989). The fact that inhibition occurred at high concentrations of NH_4–N but not at low concentrations is consistent with this mechanism. A low level of glutamine synthetase activity would allow uptake and assimilation of low NH_4–N concentrations from the 0.25 nutrient solution, but the high NH_4–N concentrations immediately following treatment with the 2.0 nutrient solution may have exceeded the plant's enzymatic capacity and thus had toxic effects on the plants.

Effects of Solution Nitrogen Concentration on Productivity

Aboveground DM production of *E. lanceolatus* was consistently enhanced by increased nitrogen availability, whereas that of *O. hymenoides* was not. The difference between

O. hymenoides and *E. lanceolatus* cannot be attributed simply to differences in their native habitats, to differences in growth form, to differences in storage of nitrogen within tissues, or to low supplies of soil nitrogen. Plants from less fertile sites are often less responsive to nutrient supply than those from more fertile environments (Chapin 1980). Although *O. hymenoides* is generally found on slightly coarser soils than *E. lanceolatus*, both species intermingle in the area from which we collected the *O. hymenoides* plants. It is also very unlikely that the cultivar of *E. lanceolatus* used in our greenhouse experiment was inadvertently selected for response to applied nitrogen for three reasons. First, the original accession for Sodar was a naturally occurring variety, and field trials were conducted on native, unfertilized soils. Second, the cultivar was released for its ability to form a groundcover under dry conditions rather than for its forage production (Douglas and Ensign 1954). Third, our field experiments with native plants of both species show similar results (Smith and Nowak 1990, Nowak et al. manuscript). Thus, these two species share similar habitats but differ in their response to nitrogen supply. The differences in nitrogen response between the rhizomatous grass *E. lanceolatus* and the bunchgrass *O. hymenoides* also cannot be attributed to a difference in growth form. For example, other Great Basin bunchgrasses such as *Agropyron cristatum* (Holechek 1982), *A. desertorum* (Sneva 1973), and *Stipa thurberiana* (Miller et al. 1991) have increased DM production with nitrogen fertilization. Thus, at least some grasses of each growth form in the Great Basin respond to nitrogen fertilization. Luxury consumption, i.e., resource acquisition in excess of resource use for current growth, is a mechanism in plants from nutrient-poor environments to acquire and store nutrients for future growth (Bloom et al. 1985). In our study, tissue nitrogen concentrations of both species increased with increased level of nitrogen in the nutrient solution. Thus, the increased nitrogen concentration in tissues appears to be a generalized response of both grass species to increased nitrogen availability rather than a mechanism to acquire and store nitrogen for future growth. Finally, low rates of nitrogen application or loss of fertilizer nitrogen may preclude a fertilization response in field experiments. Because soil nitrogen content of *O. hymenoides* pots was at least twice that of pretreatment nitrogen contents and because soil nitrogen increased with increased solution nitrogen concentrations, soil nitrogen supply did not limit *O. hymenoides* growth.

The most parsimonious explanation for this difference between species in their response to nitrogen supply is that *O. hymenoides* has inherently low growth rates. Even under the nearly ideal growth conditions in our greenhouse experiment, low levels of solution nitrogen were adequate for *O. hymenoides* growth. The relatively high nitrogen content of *O. hymenoides* leaves (4–5%) also indicates that nitrogen supply was adequate. The low growth rates of *O. hymenoides* are partially due to meristematic limitations. For example, the proportional increase in tiller density from the 0.25 to the 2.0 level of nitrogen was almost three times greater for *E. lanceolatus* than for *O. hymenoides*. Intercalary meristems of *O. hymenoides* were also limited: the size of individual leaves was not significantly affected by the nitrogen solution, whereas that for *E. lanceolatus* progressively increased with the nitrogen content of the nutrient solution.

DM allocation also differed between species. Root:shoot ratios of *E. lanceolatus* plants decreased with increased nitrogen content of the nutrient solution, but nitrogen concentration did not affect belowground DM production of either species. Thus, the decreased root:shoot ratios for *E. lanceolatus* are primarily due to the increase in aboveground DM with increased nitrogen concentration. However, the lack of an effect of nitrogen availability on root production may be an artifact of the limited rooting volume in the pots. For example, results from field experiments with *E. lanceolatus* differed from our greenhouse experiment: root production and root:shoot ratios increased with fertilization in the field (Holechek 1982).

Changes in DM production and allocation can be primarily attributed to nitrogen concentration in the nutrient solutions rather than to other soil chemical properties. Although EC and cation concentrations of the soils increased with the nitrogen content of the nutrient solutions, EC values were within the range that does not show any adverse effect for many forage species (Western Fertilizer Handbook 1985). Furthermore, both *O.*

hymenoides and *E. lanceolatus* tolerate low to moderate salinity (Douglas and Ensign 1954, Robertson 1976). Because the concentrations of most other ions were kept constant in the nutrient solutions, variation in the concentrations of other nutrients also did not confound the experiment.

In summary, these two co-existing, perennial grasses from semiarid habitats in the Great Basin respond differently to both form and amount of plant-available nitrogen under ideal growth conditions. Physiological responses to nitrogen fertilization in field experiments also differed among species from the same vegetation type (Toft et al. 1989). These results indicate that the variation in responses to nitrogen fertilization in field trials may be partially due to species-specific characteristics. Thus, procedural problems alone do not account for the lack of response to nitrogen fertilization in field trials. The extent to which these differential, species-specific responses to nitrogen influence community dynamics is unknown, but warrants further study.

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LITERATURE CITED

BARKWORTH, M. E., AND D. R. DEWEY. 1985. Genomically based genera in the perennial Triticeae of North America: identification and membership. American Journal of Botany 72: 767–776.

BLOOM, A. J., F. S. CHAPIN III, AND H. A. MOONEY. 1985. Resource limitation in plants—an economic analogy. Annual Review of Ecology and Systematics 16: 363–392.

BOLLARD, E. G. 1966. A comparative study of the ability of organic nitrogenous compounds to serve as the sole sources of nitrogen for the growth of plants. Plant and Soil 25: 153–166.

CHAPIN, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233–260.

CHIARIELLO, N. R., H. A. MOONEY, AND K. WILLIAMS. 1989. Growth, carbon allocation and cost of plant tissues. Pages 327–365 *in* R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, eds., Plant physiological ecology, field methods and instrumentation. Chapman and Hall, New York.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, J. L. REVEAL, AND P. K. HOLMGREN. 1977. Intermountain flora: vascular plants of the Intermountain West, USA. Vol. 6. Columbia University Press, New York.

DOUGLAS, D. S., AND R. D. ENSIGN. 1954. Sodar wheatgrass. Idaho Agricultural Experiment Station Bulletin N.S. 234.

FAIRBOURN, M. L., AND F. RAUZI. 1982. Effect of annual low-nitrogen fertilization of crested wheatgrass. Soil Science 134: 126–132.

FITTER, A. H., AND R. K. M. HAY. 1987. Environmental physiology of plants. 2nd ed. Academic Press, London.

GOMEZ, K. A., AND A. A. GOMEZ. 1984. Statistical procedures for agricultural research. John Wiley and Sons, New York.

HITCHCOCK, C. L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

HOLECHEK, J. L. 1982. Fertilizer effects on above- and belowground biomass of four species. Journal of Range Management 35: 39–42.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187–211.

JAMES, D. W., AND J. J. JURINAK. 1978. Nitrogen fertilization of dominant plants in the northeastern Great Basin desert. Pages 219–231 *in* N. E. West and J. J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

JONES, T. A. 1990. A viewpoint on Indian ricegrass research: its present status and future prospects. Journal of Range Management 43: 416–420.

KLUBEK, B., P. J. EBERHARDT, AND J. SKUJINS. 1978. Ammonia volatilization from Great Basin desert soils. Pages 107–129 *in* N. E. West and J. J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

MACMAHON, J. A., AND D. J. SCHIMPF. 1981. Water as a factor in the biology of North American desert plants. Pages 114–117 *in* D. D. Evans and J. L. Thames, eds., Water in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

MAGALHAES, J. R., AND D. HUBER. 1989. Ammonium assimilation in different plant species as affected by nitrogen form and pH control in nutrient solution. Fertilizer Research 21: 1–6.

MILLER, R. F., P. S. DOESCHER, AND J. WANG. 1991. Response of *Artemisia tridentata* ssp. *wyomingensis* and *Stipa thurberiana* to nitrogen amendments. American Midland Naturalist 125: 104–113.

RICHARDS, L. A. 1954. Diagnosis and improvement of saline and alkali soils. United States Department of Agriculture, Agricultural Handbook No. 60.

ROBERTSON, J. H. 1976. The autecology of *Oryzopsis hymenoides*. Mentzelia 2: 18–27.

SKUJINS, J. 1981. Nitrogen cycling in arid ecosystems. Pages 477–491 *in* F. E. Clark and T. Rosswall, eds.,

Forest soil nitrogen cycle processes, strategies and management impacts. Swedish National Science Research Council, Stockholm.

SMITH, G. S., C. M. JOHNSTON, AND I. S. CORNFORTH. 1983. Comparison of nutrient solutions for growth of plants in sand culture. New Phytologist 94: 537–548.

SMITH, S. D., AND R. S. NOWAK. 1990. Physiological ecology of plants in the Intermountain lowlands. Pages 179–241 *in* C. B. Osmond, L. F. Pitelka and G. M. Hidy, eds., Plant biology of the Basin and Range. Ecological Studies Vol. 80. Springer-Verlag, New York.

SMUCKER, A. J. M., S. L. MCBURNEY, AND A. K. SRIVASTAVA. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agronomy Journal 74: 500–503.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames.

SNEVA, F. A. 1973. Crested wheatgrass response to nitrogen and clipping. Journal of Range Management 26: 17–50.

THOMAS, R. J., K. A. B. LOGAN, AND A. D. IRONSIDE. 1987. Effects of nitrogen source on root-induced pH changes around grass and clover roots. Journal of Plant Physiology 128: 189–192.

TOFT, N. L., J. E. ANDERSON, AND R. S. NOWAK. 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. Oecologia 80: 11–18.

VESSEY, J. K., L. T. HENRY, S. CHAILLOU, AND C. D. RAPER, JR. 1990. Root-zone acidity affects relative uptake of nitrate and ammonium from mixed nitrogen sources. Journal of Plant Nutrition 13: 95–116.

WARD, K. J., B. KLEPPER, R. W. RICKMAN, AND R. R. ALLMARAS. 1978. Quantitative estimation of living root wheat-root lengths in soil cores. Agronomy Journal 70: 675–677.

WESTERMAN, R. L., AND T. C. TUCKER. 1978. Denitrification in desert soils. Pages 75–106 *in* N. E. West and J. J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

WESTERN FERTILIZER HANDBOOK. 1985. Interstate Printers and Publishers, Danville, Illinois.

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